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Distribution and Abundance of Terrestrial Snails in Three Habitat Types in Southwestern Alberta

by

Osvaldo Locasciulli

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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Abstract

Some species of terrestrial gastropods can host larval stages of lungworms (*Protostrongylus* spp.), which have been linked with periodical die-off in herds of bighorn sheep (*Ovis canadensis*). The distribution and abundance of some terrestrial snails, indicated as suitable intermediate hosts for those lungworms, were analysed in this study. In particular, it was predicted that the horizontal distribution of the snails would be clumped, and that their abundance would decrease proportionally with the depth at which the samples are collected; that the presence of snails in the soil would be positively correlated with the presence of organic matter and not correlated with the understorey vegetation. Between May and August 1980 and 1981, fourteen species of pulmonate snails were recovered by wet-sifting 600 core samples of soil, collected from three habitat types in a bighorn sheep range in the foothills of southwestern Alberta. The three habitat types (Poplar stand, Mixedwood and Spruce forest) contributed considerably different proportions to the total number of gastropods collected (33.7%, 7.6% and 58.7%, respectively), and in most cases the gastropods were highly clumped in their horizontal distribution. There were little temporal differences in the number of snails collected. The presence of snails was positively correlated with the presence of organic litter, and their abundance decreased proportionally with the soil depth. A considerable proportion (ca 42%) of gastropods was recovered from soil samples collected below 5 cm. The vertical distribution of the snails varied temporally, with increasing proportions of gastropods being found in the top 5 cm of soil from May to August. Presence of molluscs was not correlated with understory vegetation, and some species were more abundant than others in the three habitat types. In particular, members of the Pupillidae (the most abundant family in all the three habitat types) were found in different proportions in the three habitat types: *Vertigo gouldi* was most abundant in the Poplar stand, whereas, *V. modesta*, and *Columella* spp. were recovered mostly from the Spruce forest. Members of two other families (Endodontidae, and Zonitidae) were much less abundant than the Pupillidae, and showed less variation in their proportions in the three habitat types. Precipitation was not correlated with snail distribution, whereas, the increasing mean temperature, from May to August, might have played a role in the increasing proportions of snails in the top layers of the soil.

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Table of Contents

I. GENERAL INTRODUCTION 1

II. STUDY AREA 3

III. GENERAL METHODS 6

Justification 8

IV. HORIZONTAL AND VERTICAL DISTRIBUTION OF TERRESTRIAL SNAILS IN THREE HABITAT TYPES 16

Introduction 16

Methods 16

Results 17

Discussion 23

V. THE RELATIONSHIP BETWEEN TIME, VEGETATION AND CLIMATE, AND THE VERTICAL DISTRIBUTION OF TERRESTRIAL SNAILS IN THREE HABITAT TYPES IN SOUTHWESTERN ALBERTA 25

Introduction 25

Methods and Materials 26

Results 26

Discussion 27

VI. CONCLUDING DISCUSSION 41

VII. LITERATURE CITED 43

VIII. APPENDIX 47

List of Tables

Table		Page
1.	Number of snail shells collected from three habitat types in the Sheep River Wildlife Sanctuary, in southwestern Alberta, in 1980 and 1981	18
2.	Proportions of gastropods at four depths in the soil, in three habitat types, in the Sheep River Wildlife Sanctuary, in southwestern Alberta. Data for years and months combined	19
3.	Number of gastropods from three habitat types, in the Sheep River Wildlife Sanctuary, in southwestern Alberta at four depths in the soil. Data for years combined.	20
4.	X^2 analysis of the association between terrestrial gastropods and litter, in the Sheep River Wildlife Sanctuary, in southwestern Alberta.	21
5.	X^2 test for the horizontal distribution of land snails, in the Sheep River Wildlife Sanctuary, in southwestern Alberta	22
6.	Numbers and proportions of different species of terrestrial snails, from three habitat types, in the Sheep River Wildlife Sanctuary, in southwestern Alberta	28
7.	Average size of different species of terrestrial molluscs from three habitat types in the Sheep River Wildlife Sanctuary, in southwestern Alberta	29
8.	Multiple correlation between numbers of snails and coverage of ground vegetation in the Sheep River Wildlife Sanctuary, in southwestern Alberta	30

List of Figures

Figure — Page

1. The statistical analysis used in this study 8
2. Variations in numbers of shells / sample and in the number of species recovered, as sample size is increased 14
3. Vertical distribution of terrestrial snails in the Poplar stand, in the sheep River Wildlife Sanctuary, in southwestern Alberta, in 1980 and 1981 32
4. Vertical distribution of terrestrial snails in the Mixedwood, in the sheep River Wildlife Sanctuary, in southwestern Alberta, in 1980 and 1981 34
5. Vertical distribution of terrestrial snails in the Spruce forest, in the sheep River Wildlife Sanctuary, in southwestern Alberta, in 1980 and 1981 36
6. Precipitation and mean temperatures, from May to August, recorded in the study area 39

I. GENERAL INTRODUCTION

Bighorn sheep (*Ovis canadensis*) are commonly infected with nematode parasites that, from time to time, produce pathologic conditions in the lungs of their definitive host (Pillmore 1958, Buechner 1960). The two species of nematodes associated with this problem, *Protostrongylus stilesi* and *Protostrongylus rushi*, use terrestrial gastropods as intermediate hosts. Species of the families Pupillidae, Valloniidae and Zonitidae are implicated in this role (Forrester 1971, Latson 1977); however, the link in the nematode life cycle between the sheep, which pass first stage larvae (L1s) in their feces, and the gastropods remains poorly understood (Blood 1963, Forrester 1971, Lange 1973, Latson and Woodard 1979). Also, the link between the gastropods, in which the L1 larvae grow to third stage larvae (L3s), and the sheep (Pillmore 1958, Forrester 1971, Latson 1977), is not certain. To determine how these links are forged it is necessary to understand more fully the ecology of the gastropod intermediate hosts, particularly their distribution in space and time.

Boag and Wishart (1982) recorded 15 species of terrestrial gastropods on the winter range of a population of bighorn sheep in southwestern Alberta. Their data were based on living snails found attached to a series of masonite squares put down in a number of different habitats. Boag and Wishart (1982) did not quantify in detail how the distribution of snails varied within habitats, apart from showing that numbers change in ecotonal situations. Like most ecological studies of terrestrial gastropods (for example Uminski and Focht 1979, Platt 1980, Van Es and Boag 1981), Boag and Wishart (1982) did not consider the vertical distribution of the gastropods, nor the extent to which two or more species were associated in the same litter layer, within habitats. Indeed, many studies of terrestrial gastropods (for example, Uminski 1979, Platt 1980, Van Es and Boag 1981) appear to be based on the assumption that the gastropods are evenly distributed in the upper litter layer of the soil. This assumption needs to be validated because, if incorrect, it may lead to inaccurate population estimates, and to inaccurate interpretations of the gastropods life histories. The need to be aware of biases inherent in certain sampling techniques has been pointed out by Bishop (1977) and Boag (1982).

This study was undertaken to provide a quantitative analysis of the spatial distribution of land snails present on a bighorn sheep range in the foothills of

southwestern Alberta, an area used by a herd of bighorn sheep in winter. Not only were the two surface dimensions considered, but also a third, the vertical dimension down into the litter, was examined.

The specific objectives were: 1) to identify the species of land snails associated with three major habitat types in the area; 2) to determine the distribution of these snails, both horizontally and vertically, over the frost-free season in 2 years (1980 and 1981); 3) to determine the extent to which the various species of snails were associated in time and space, and the extent to which these associations reflected edaphic, vegetational and climatic factors; 4) to compare the sampling procedure used with others reported in the literature.

II. STUDY AREA

This study was carried out in southwestern Alberta, in the Sheep River Wildlife Sanctuary, within the Bow-Crow Forest Reserve, about 60 km SW of Calgary. This sanctuary, located in the foothills at an altitude of ca 1400 m, is used by a herd of bighorn sheep (*Ovis canadensis*) especially during winter and spring. A variety of plant communities is present, reflecting different topographic and edaphic conditions. Stands of lodgepole pine (*Pinus contorta*), the result of past fires (Ogilvie 1969), dominate much of the area. The south- and west-facing slopes, and old river benches, support *Festuca-Danthonia* grasslands that are dissected by stands of trembling aspen (*Populus tremuloides*) wherever topography creates a moister habitat. On the valley floor there are areas characterized by poor drainage where white spruce (*Picea glauca*) communities in various successional stages are found. Many of the habitat types in the sanctuary have been sampled regularly for gastropods since 1979 (Boag 1979, Boag and Wishart 1982).

I chose three habitat types in the sanctuary (Poplar, Mixedwood, and Spruce), within each of which, I established a 1-ha grid with 20-m intervals. The Poplar community was located on a south-facing slope, to the north of a grassy river bench, at an elevation of ca 1500 m. This was an aspen-dominated community, commonly found in such locations along the foothills (Ogilvie 1969). The stand was completely surrounded by grassland. The tree layer was dominated by trembling aspen (*Populus tremuloides*) which formed a closed canopy over most of the area sampled. Balsam poplar (*Populus balsamifera*) and white spruce (*Picea glauca*) were present in a wetter zone (a draw through which two intermittent streams flowed). The shrub layer was poorly represented, with scattered wild rose (*Rosa woodsii*), snowberry (*Symphoricarpos albus*), willows (*Salix* spp.), meadowsweet (*Spirea densiflora*), and shrubby cinqfoil (*Potentilla fruticosa*). *Rosa* was the only genus contributing significantly to the shrub coverage (ca 5%) within the gridded area (see Appendix I). The herb layer was strongly dominated by grasses (mostly *Elymus canadensis*(?)) with a coverage ranging from ca 45 % to ca 68 % (Appendix I). In the northern section of the sampled area, where the overstorey canopy was open, *Solidago canadensis* was present. *Epilobium angustifolium* also covered large portions of the ground (ca 18 %: Appendix I). Other plants recorded frequently included: *Smilacina stellata*, *Aster* spp., *Fragaria virginiana*, *Heracleum lanatum*,

Lathyrus ochroleucus, *Geranium* spp., *Thalictrum venulosum*, and *Galium boreale* (Appendix I). The soil is brunisoil (Ogilvie 1969) with the litter layer 5 to 7 cm thick, and with the humus layer of about the same thickness. The whole area is on an overall gentle slope, with the exception of the northeastern edge, which inclines to about 45°. The southeastern and the southwestern edges of the grid included a portion of the surrounding grassland, providing an ecotone between this and the Poplar stand itself. A thermograph (Peabody Ryan model 'J') was placed flush with the soil in this area from September 1980 to January 1981, and from March 1981 to August 1981.

The Mixedwood community, located on an upper river bench, was a successional community characterized by great heterogeneity in vegetative cover. The terrain was generally flat and well drained at an elevation of ca 1500 m, but the southeastern portion was about 5 m higher than the rest, and comprised about a third of the total area sampled. The soil upper horizons were very thin, and the *A* horizon (Foth 1978) ranged from 2 to 4 cm at lower altitude, and from 0 to 2 cm at the higher elevation. The *B* horizon was very rocky, especially at the higher elevation, and included stones of various size which appeared to be rich in calcium carbonate content. A 1-ha grid established in this community included an area where the composition of the tree layer graded from a rather homogeneous stand of lodgepole pine (*Pinus contorta*) towards an association of deciduous (*Populus balsamifera* and *P. tremuloides*) and coniferous trees (*Picea glauca* and *Pinus contorta*). The canopy was generally open, with the exception of the northwestern edge of the grid, where a closed canopy of *Pinus* and/or *Populus* was found.

The shrub layer was reasonably well represented, especially at the higher elevation, where buffalo-berry (*Sheperdia canadensis*) and wild rose (*Rosa woodsii*) were common (Appendix I). The herb layer was moderately abundant at lower elevation but poorly represented in the higher locations. Overall, the plants in this layer tended to be shorter than in the comparable layer in the Poplar stand. This was especially true of the Gramineae, the average height of which was about half that of the grasses in the Poplar stand. Their coverage was also less, with a maximum recorded value of ca 24 % in July (Appendix I). Nevertheless, the Gramineae formed the dominant taxon, although their dominance was not as pronounced as in the Poplar because of the greater variety and

more even distribution of taxa in this habitat type (Appendix I). Bryophytes were noticeably more abundant, up to 9 % of coverage, although they were generally absent at the higher elevation. The opposite trend was shown by the lichens, which tended to be more frequent in the dry elevated locations, with coverage ranging up to ca 6 %. Virtually all the taxa present in the Poplar forest were also present in the Mixedwood. Other taxa frequently encountered, but not recorded in the Poplar stand, were: *Anemone patens*, *Mitella pentandra*, *Hedysarum* spp., *Cornus canadensis*, *Monesia uniflora*, *Pyrola* spp., *Arctostaphylos uva-ursi*, *Mertensia paniculata*, *Linnaea borealis*; and *Arnica cordifolia*.

The Spruce community, reportedly a climax forest (Ogilvie 1969), was dominated by white spruce (*Picea glauca*). It was located on a flat bench above a canyon cut by the Sheep River, at an elevation of ca 1500 m. A few old balsam poplars (*Populus balsamifera*) were still present in this poorly drained area, relics from an earlier stage in the succession. The canopy was generally closed. The western part of the area was crossed by a network of small streams. The litter layer, when present, was composed mainly of spruce needles and decaying wood, and varied in thickness from 0 to, at least, 30 cm in some locations. The rest of the *A* horizon was well represented throughout the area, being, at least, 15 cm thick. Sampling down the 20 cm, in this area I never reached the *B* horizon.

The shrub layer was poorly represented, with only a few scattered willows, buffalo-berry, raspberry (*Rubus* spp.), wild rose, and gooseberry (*Ribes* sp.).

In the low understorey layer, grasses were present, although poorly represented and always in poor conditions of growth, with no evidence of flowering. Most of the ground was covered by a mat of Bryophytes, often associated with *Equisetum arvense*, particularly in the wetter western part of the grid. Relatively large areas of bare ground covered only by litter, were present in the eastern part of the grid. Lichens were sometimes found on the ground, either covering the litter or in association with mosses, but their coverage never exceeded 6% (Appendix I). Other plants regularly encountered in this habitat type were: *Mitella pentandra*, *Fragaria virginiana*, *Lathyrus ochroleucus*, *Geranium* spp., *Epilobium angustifolium*, *Cornus canadensis*, *Monesia uniflora*, *Pyrola* spp., *Mertensia paniculata*, *Linnaea borealis*, *Aster* spp., *Petasites palmatus*, and *Taraxacum officinale*.

III. GENERAL METHODS

At the end of each of 4 months (May to August), I collected 25 litter samples from each of the three habitat types, for 2 consecutive years (1980 and 1981).

The locations where the samples were taken were determined by using calculator-generated random numbers (Texas Instrument TI 59: ML 12). The coordinates on the 1-ha grid were measured from reference points (established in the grid at 20-m intervals) with a compass and tape-measure.

Samples were taken with a steel corer of diameter 6.2 cm and length 20.0 cm.; each core being subdivided into 4 subsamples of 5 cm in depth, from top to bottom. These were referred to as I, II, III and IV, regardless of their composition: LI was composed mostly of litter. When the litter was <5 cm thick, I included some from the immediately surrounding area, to make up a volume equivalent to that in the first 5 cm of the corer. At each location, 4 cores were taken so that the subsamples (I, II, III, and IV) came from separate cores. In this way, the subsamples of the cores were statistically sample-independent of one another. Samples were placed in plastic bags and kept at ambient temperature until processed. To assess the degree of deterioration of snail shells under these conditions, I prepared artificial samples with a known number of measured fresh snails of several species in each.

To process the samples, I used a wet-sifting technique (Newell 1971). By this method, soil particles were washed through a set of sieves of decreasing mesh width, and the residue dried with a 1500-watt fan-heater. The residue that collected on the sieves with larger mesh width (from 10 to 2 mm) was hand-sorted, whereas the residue on the last sieve (mesh = 0.77 mm) was examined with the aid of a dissecting microscope (Wild M5) at 6X power. To determine whether the presence of litter in the subsample was correlated with the presence of snails, I estimated the volume of litter in each subsample by assigning a value of 1 to subsamples containing an estimated 30%, or more, of decaying leaves and wood particles, and a value of 0 to those subsamples estimated to have less than 30% litter.

Identification of the recovered gastropods was based on Pilsbry (1946, 1948) and Burch (1962). Only those shells which appeared to be fresh, with no sign of erosion, were included in the analyses. Voucher specimens of all species recovered have been

deposited in the Museum of Zoology, University of Alberta.

Using a quadrat sampling technique (Kershaw 1966), I quantitatively assessed the abundance of vegetation in the shrub and herb layers. Using a rectangular metal frame (20 x 50 cm), I estimated the area inside the frame covered by the perpendicular projection of the crown on the soil (Daubenmire 1968), for each taxon, for all plants with a diameter < 1 cm at breast height. This procedure was done twice at each of the sites selected for coring, before the cores were taken. The plants were identified *in situ*, using Moss (1977), and checked against previously identified herbarium specimens housed at the R. B. Miller Biological Station.

The data analysis was subdivided into four main parts (Figure 1). In the first part, I tested the differences in density of snails among the three habitat types during the four months of the sampling period (May to August), and between the 2 years, 1980 and 1981, as well as differences in the vertical distribution of the snails in the four subsamples (I, II, III, and IV). The objective of part two was to consider the association between the snails and the litter in each subsample. The third part dealt with the dispersion pattern in the horizontal distribution of the snails in each of the habitat types. In the fourth part, I considered the relationship between the presence of snails and the coverage of each of the plant taxa recorded in the sampling sites.

Since several statistical tests were performed on the same set of data, the critical level of significance was adjusted accordingly, using the formula $\alpha = 1-(1-P)^n$, after Kirk (1968), in which α is the overall level of significance, P the probability for each of the tests performed and n the number of tests performed.

Justification

Soil sampling

In choosing the locations from which to take the core samples, I used a simple random sampling procedure (Steel and Torrie 1960), based on the findings from a preliminary study carried out in August 1979 (Boag 1979). Random samples were taken in the litter layer of three different habitat types: Grassland (on a flat river bench), Poplar stand, and Mixedwood (referred to as Pine by Boag, 1979). Since the distribution of the gastropods seemed to be clumped, and their abundance to be greater in forested areas

Figure 1. The statistical analysis used in this study

α *overall*=0.05

α_1=0.0127	α_1=0.0127	α_1=0.0127	α_1=0.0127
1) Density differences for gastropod shells among: 2 years, 3 habitat types, 4 months. (*ANOVA*: split-plot) α_2=0.0064 2) Density differences of gastropod shells, at 4 depths in the soil. (Friedman's *ANOVA* by ranks) α_2=0.0064	Association between the presence of snails and the presence of litter (X^2 test).	X^2 test for the horizontal distribution (clumped *vs* Poisson) of the snails in the three habitat types. (12 tests). α_2=0.0011	Multiple correlation analysis between the coverage values of understorey vegetation and the number of snails of the different species.
Part 1	Part 2	Part 3	Part 4

α *overall*= overall level of significance.
α_1= level of significance for the first level.
α_2= level of significance for the second level.

than grasslands (Boag 1979; Boag and Wishart 1982), I concluded that random sampling, within a grid located in a forested area, was the most appropriate method for achieving a representative picture of the distribution of the gastropods.

The samples taken in this preliminary test measured 30 X 30 X 8 cm. As a consequence, they comprised, mostly, litter. The low number of specimens recovered from these samples suggested that a relatively large number of samples was necessary to achieve an appropriate level of confidence in the results. A large number of samples would also insure a satisfactory coverage of a study area that was heterogeneous in vegetation composition, canopy coverage, soil moisture and thickness of soil horizons.

A sample size of 30 is customarily considered appropriate for statistical analysis. In fact, Hairston *et.al.* (1958) recommend that 30 or more samples should be taken from each habitat, and that the volume of the samples should be small. Bishop (1977) considers 30 samples as appropriate to start a quantitative investigation on gastropods. Since I was interested in studying three different habitat types for 2 years, during 4 months each year, I decided that reducing the sample size to 25, instead of 30, would be a reasonable compromise, without impairing the statistical analyses, yet reducing processing time. I also estimated that, for the samples, a core of about 600 cc (divided into four equal subsamples) was the minimum necessary to insure the recovery of a meaningful number of snails. To determine the vertical as well as the horizontal distribution of snails, I decided to sample to a depth of 20 cm.

Choice of technique for analyzing the samples

I chose to sift the soil with the aid of water for a number of reasons. First, techniques suitable for recovering other invertebrates, such as the Berlese funnel (Berlese 1905), which involves applying a suitable repellent stimulus causing the animals to move away into a container, are unsuccessful when applied to terrestrial gastropods (Newell 1971). These animals usually just build an epiphragm and undergo dormancy under the adverse conditions.

A second method, of slowly flooding test samples with cold water (Beyer and Saari 1978, Kralka 1983), was tested and abandoned. It proved time consuming and required an abundance of space when dealing with many samples. Moreover, upon sifting the soil after flooding, I found a number of snails that had not emerged from the soil.

These were mostly small members of the Pupillidae, and, although I did not carry out any statistical analysis, I judged their number to be too high for a satisfactory quantitative analysis of the number of molluscs present in the samples. This technique, however, has proven satisfactory when dealing with smaller number of samples, and for larger species of snails, such as *Vallonia gracilicosta* and *Discus cronkhitei* (Kralka 1983).

I also decided not to use a technique I devised, which was based on an observable response of some snails in a terrarium. Under humidity conditions above the dew point and at the temperature of 22±2 °C, all species of snails in the terrarium tended to emerge from the soil and move vertically up the walls of the terrarium, or onto twigs, pine needles, or any other vertical objects available. They moved vertically, apparently in an attempt to find a more suitable microclimate (Cameron 1970). Sifting the soil later, however, revealed a number of snails which had not emerged. Nonetheless, this technique deserves further investigation, and it may prove useful when fewer samples are considered. It requires little labor, and allows the recovery of living snails, and, possibly, slugs. On the other hand, its efficiency needs to be assessed (Newell 1971, Kralka 1983) before it could be used in studies involving population estimates.

Techniques based on attracting molluscs under some shelters, such as pieces of wet corrugated cardboard (Lankester and Anderson 1968), or masonite, with or without wet corrugated cardboard (Boag and Wishart 1982), must rely on assumptions that, to date, have not been investigated. In particular, in obtaining an unbiased estimate of the population, using these techniques, it is necessary that all species of gastropods are equally attracted by the shelter used, and that, within each species, the probability of being attracted (and collected) is the same for all individuals. It must also be assumed that the attractivness of the shelter is independent of the gastropod's age, physical and physiological condition; and, that it is not affected by the depth at which the molluscs are located in the soil at the time of sampling, nor by the edaphic factors prevailing below the shelter. These techniques are useful and convenient when there is the necessity of collecting living gastropods for taxonomic or experimental purposes. But, when population estimates are involved, they should be used with some caution. To date, I know of no evidence to support the assumptions mentioned above.

I considered inappropriate to this study, those techniques in which only the upper layers of the soil were sampled (for example, Karlin 1961; Uminski 1979, Platt 1980, Van Es and Boag 1981). In fact, only those molluscs present in the superficial layers at the moment of sampling can be recovered. I believe that the biases associated with these sampling techniques (Bishop 1977, Boag 1982), may severely impair estimates of population size.

Flotation techniques based on differential gravity of material are not suitable for soils rich in organic matter (Hale 1964), as were my samples. I found other flotation methods, specifically designed for recovering snails (Coney *et al*. 1981), impractical and time consuming, especially for a large number of samples. Additionally, these techniques require the use of hazardous substances, like xylene.

The samples taken in the preliminary field test were sifted after being air-dried. With this technique I often found snails adhering to particles of organic or inorganic matter. These particles often occurred as lumps of various size, inside which I sometimes found snails. Breaking down the lumps increased processing time, and, invariably, resulted in the breaking of some shells. Even very fresh shells were broken. In fact, I often found fragments with no sign of erosion and with dry body tissue attached.

Snails were usually not damaged using the wet-sifting technique. The only gastropods I know I could not recover with this technique were the slug *Deroceras laeve* and the snail *Vitrina alaskana*. *Vitrina alaskana* has a shell that is extremely thin, and too fragile, even for the wet-sifting technique. Since *Deroceras laeve* and *Vitrina alaskana* are not included amongst the gastropods indicated as suitable intermediate hosts of *Protostrongylus* spp. (Forrester 1971; Latson 1977), and since I could not recover those molluscs using any other sifting technique that I am aware of, I decided not to include them in my study.

The examination of the artificial samples prepared to assess shell deterioration (see General Methods), suggests that with the wet-sifting technique it is possible to process soil samples a long time after they have been collected, if properly stored. In fact, the test-shells of all species included in the samples, showed no detectable deterioration up to a storage period of 10 months, at ambient temperature. I attributed this to the fact that the water in the samples evaporated quickly, in 1 or 2 weeks, under

the conditions at which I kept them. I believe that mechanical damage to the shells was virtually prevented by the storage conditions, and, that the lack of moisture in the soil samples greatly reduced the chemical decomposition of the shells.

Increasing the distance between the fan-heater and the wet residue on the sieve, allows the recovery of living snails, but this increases processing time, and the samples must be sifted immediately after collection to avoid the death of the gastropods.

Relationship between snail abundance and canopy cover.

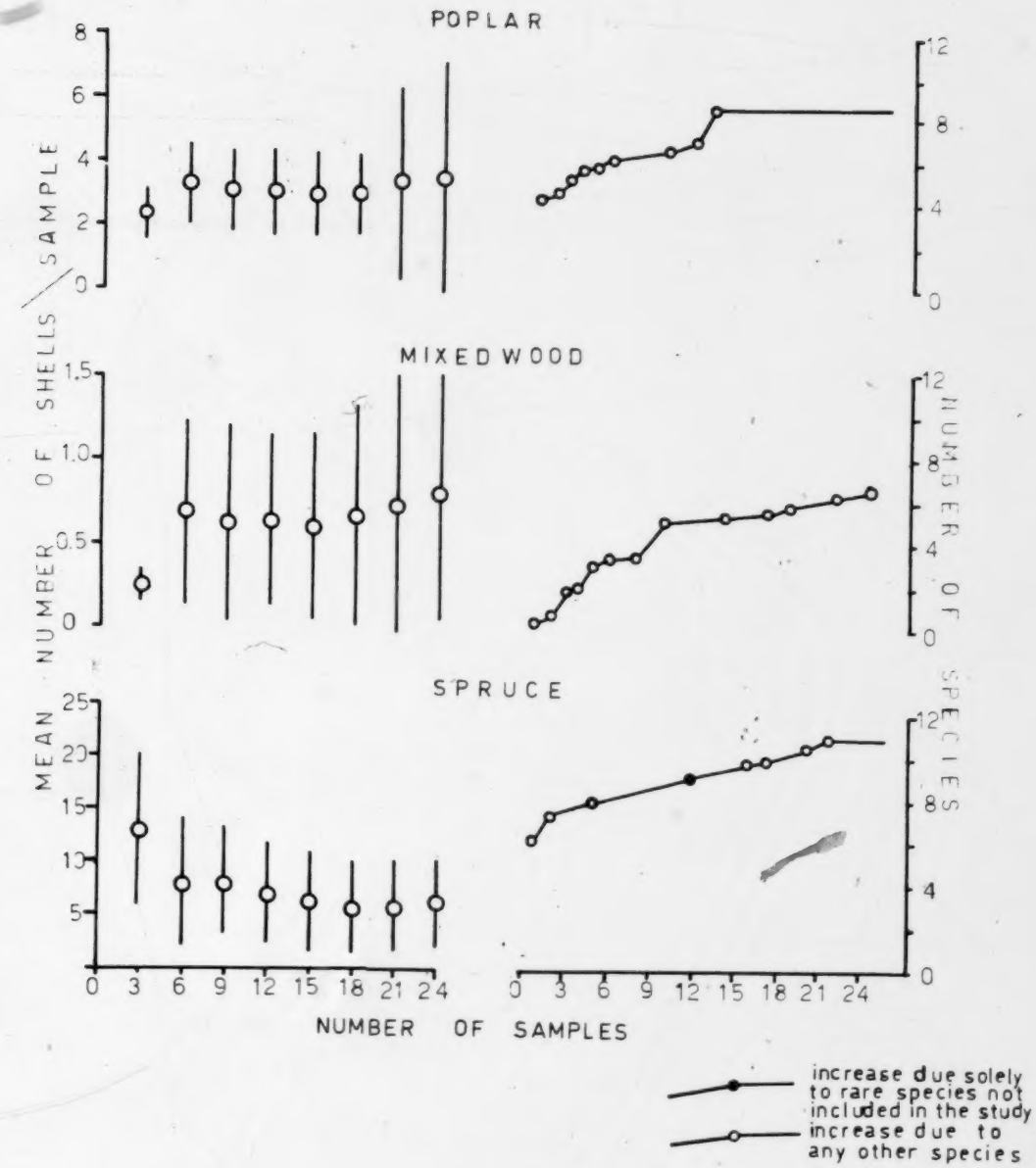
Examining the samples from a preliminary study (Boag 1979), I formulated the hypothesis that the number of snails in the soil was positively correlated with the presence of litter. This layer is composed mostly of decaying leaves and twigs (Foth 1978), possibly explaining why Platt (1980), Van Es and Boag (1981), and Boag and Wishart (1982) often found a significantly higher number of snails in forested areas, where the litter is more abundant than in the grasslands (Odum 1970), than they did in treeless areas.

Trees are the main contributors, with their leaves, to the formation of the litter (Lutz and Chandeler 1946). For this reason, I initially measured the canopy directly above the sampling sites, using photography (Johnson and Vogel 1968). Later, I discarded this method because I found areas with no canopy above them, in which a thick litter layer was present (*e.g.*, clearings and ecotones). Since I intended to test the hypothesis that the presence of snails was directly dependent on the litter, I chose to measure the last directly, even if perhaps more crudely (see General Methods).

Effects of the sample size on the reliability of the results.

Using the data obtained from sifting 600 core soil samples (see section V), collected from three habitat types in 2 years, from May to August (see General Methods), I carried out an *a posteriori* assessment of the choice of 25 as the minimum sample size necessary for this study. Each set of data, from the 25 samples collected, was assigned a new calculator-generated random sequence number, from 1 to 25 inclusive. I used the same sequence for all 12 sets of samples (results from 1980 and 1981 were combined). For each of the habitat types the samples were considered in increasing numerical order (results from the 4 months were averaged), and the total number of species recorded with each additional sample was noted, as well as the mean number of shells per sample (Figure 2).

Figure 2. Variations in the values of the mean number of shells (± 1 std dev) and in the maximum number of species recovered, as the sample size is increased.


POPLAR
MIXED WOOD
SPRUCE
MEAN NUMBER OF SHELLS / SAMPLE
NUMBER OF SPECIES
NUMBER OF SAMPLES
0 3 6 9 12 15 18 21 24
increase due solely to rare species not included in the study
increase due to any other species

Brown (1982) found, for acquatic gastropods, that most species were recovered after only five samples. Results from this study suggest that, for terrestrial gastropods, there is considerable variation in the minimum number of samples necessary to recover all the species of snails, depending upon the characteristics of the habitat type sampled (Figure 2). Walden (1981) maintains that, in the area sampled, the number of species recovered depends on the distribution of the snails. In the Poplar stand, the maximum number of species was obtained with as few as 13 samples (Fig. 2); but, in the Mixedwood and in the Spruce forest, the number of species did not cease to rise, even when a sample size of 25 was considered (Figure 2). The high values recorded for the standard deviation are due to the highly clumped distribution of the molluscs (see Section IV).

These results suggest that the minimum number of samples may be reduced considerably, in studies with a more limited scope than the present one, depending on the problems investigated. For example, if only the mean number of shells per sample is important, 6 samples may already be sufficient to give a representative picture of the gastropod population, present in all three habitat types, when the different species are combined. If the number of species is important, the number of samples may be reduced to 13, if only the Poplar stand is under investigation. However, in this study, I considered important, both the number of shells per sample, and the total number of species present in each of the three habitat types. For this reason, a minimum of 25 samples, collected from each habitat type, was appropriate to insure a reasonable estimate of the mollusc populations present (Figure 2).

IV. HORIZONTAL AND VERTICAL DISTRIBUTION OF TERRESTRIAL SNAILS IN THREE HABITAT TYPES

Introduction

The techniques used in sampling gastropods are numerous and varied, and none seems applicable to all situations (Hairston *et al.* 1958). Regardless of the technique chosen, underlying assumptions must be valid if the technique is to be reliable. Overlooking these assumptions may lead to loss of reliability in the data (Bishop 1977; Boag 1982), particularly in cases involving population estimates. Some techniques appear to be based on the assumption that the gastropods are randomly distributed in the top layer of the soil (for example, Uminski 1979, Platt, 1980). To test the validity of this assumption was one of the objectives of this study. The results of a pilot investigation carried out in the study area (Boag 1979), suggested that there was no basis for assuming a random distribution in space for members of the populations of snails sampled. On the contrary, the molluscs appeared to be highly clumped in each of the habitat types sampled. Based on these results, and on those of Boag and Wishart (1982), I formulated the hypotheses that: the gastropods were more abundant in the soil where the litter layer was well represented; 2) gastropod abundance was inversely correlated with the depth at which the sample was taken; 3) gastropod dispersion on a horizontal plane was clumped.

These hypotheses were tested with data collected in this study.

Methods

Four monthly sets of 25 core samples were taken randomly in each of three habitat types (see General Methods). In the following analyses all gastropod fresh shells were pooled, regardless of the species.

A split-plot *ANOVA* (Steel and Torrie 1960) was used to test if the number of snails recovered from the three habitat types differed among types, and among months (see General Methods). The vertical distribution of molluscs in the soil was tested using the Friedman's 2-way *ANOVA* (Zar 1974), and the relationship between snail presence and presence of litter (see General Methods) was tested using the X^2 test (Zar 1974). A test of the horizontal distribution for randomness was performed by comparing it to the

Poisson distribution, following the method suggested by Zar (1974).

For the statistical tests performed in this section, I wrote computer programs in FORTRAN, and, due to the multiple testing of the data, I adjusted the level of significance (see General Methods).

Results

Fourteen species of pulmonate gastropods were recovered from the sifted soil cores (see section V). Of these, three were basommatophoran species (*Lymnaea bulimoides*(?), *Physa gyrina*, *Planorbis* sp.) and two were stylommatophoran species (*Vitrina alaskana* , *Vallonia* sp.). All of these were rarely represented in the collections and most of their shells were deeply eroded. Excluding the above species, a total of 1858 snails was recovered from samples taken in the three habitat types over the 2 years of the study (Table 1). Of these ca 59% came from the Spruce forest, ca 33% from the Poplar stand and ca 8% from the Mixedwood, proportions which were significantly different (Table 1). The difference in the number of shells recovered between years was not significant (Table 1). On the other hand, the difference among months was significant, but with the *P* value closely approaching the critical level of significance chosen (Table 1).

A high proportion of gastropods was found below the superficial layer, especially in those locations where the litter was thick (Poplar stand and Spruce forest, see Table 2). The Spruce forest had the deepest litter layer of the three habitat types. Here, 48% of the snails were recovered from subsamples that were >5 cm below the surface of the litter. By contrast, only 10% of the snails recovered from the Mixedwood was found below the I layer in which,in this habitat type, the litter was very poorly represented (see Study Area). These differences were statistically significant (Table 3).

A X^2 analysis showed that subsamples with >30% of organic material content, yielded a significantly higher number of snails than those with little organic matter (Table 4).

The horizontal distribution of the snails recovered from the soil cores differed significantly from randomness in most months (Table 5). Since the variance was always greater than the mean, the corresponding distributions, if not significantly clumped, tended towards it (Zar 1974).

Table 1. Number of fresh shells of terrestrial gastropods from 600 core samples of soil collected from three habitat types over the frost-free season in 1980 and 1981.

	1980			1981		
	Poplar	Mixedwood	Spruce	Poplar	Mixedwood	Spruce
May	163	13	61	71	23	134
June	65	24	176	47	4	166
July	92	34	181	51	19	217
August	76	18	73	61	6	83
Total	396	89	491	230	52	600

Total number of shells = 1858

Difference between years:	F= 7.66	DF= 1, 3	*P*= 0.0670
Difference among months:	F= 44.89	DF= 2, 3	*P*= 0.0054
Difference among habitat types:	F= 15.22	DF= 2, 12	*P*= 0.0005

Based on *ANOVA* split-plot: α=0.0064

Table 2. Proportions of 1858 fresh shells of terrestrial gastropods found at 4 different depths, in 600 soil cores from three habitat types in the Sheep River Wildlife Sanctuary, from May to August 1980 and 1981. Data for years and months were combined.

Habitat Types		Poplar	Mixedwood	Spruce
Layer	Depth in cm			
I	0- 5	62%	90%	52%
II	5- 10	16%	5%	24%
III	10- 15	15%	3%	17%
IV	15- 20	7%	2%	7%
Number of shells		n= 626	n= 141	n= 1091

Table 3. Number of gastropods found in three habitat types in 600 core samples of soil at four depths (I, II, III, IV), in the Sheep River Wildlife Sanctuary, from May to August 1980 and 1981.

Depth in cm		0 <I<5	5 <II<10	10<III<15	15 <IV<20	Total
Poplar	May	88	39	73	34	234
	June	77	32	3	-	112
	July	104	28	6	5	143
	August	130	4	3	-	137
Mixedwood	May	30	1	3	2	36
	June	27	-	1	-	28
	July	50	2	-	1	53
	August	21	3	-	-	24
Spruce	May	97	43	29	26	195
	June	190	103	32	17	342
	July	173	115	93	17	398
	August	110	19	15	12	156

Difference among layers: X^2=28.7, P=0.0000, C =0.0127

I II III IV

Based on Friedman's *ANOVA*

Table 4. X^2 analysis of the association between terrestrial gastropods and litter in 600 soil cores collected from May to August, 1980 and 1981, in the Sheep River Wildlife Sanctuary, in southwestern Alberta. Each core was divided into four subsamples.[1]

	Snails	
	+	-
Organic matter[2]		
+	381	958
-	6	597

$X^2 = 194.7$, $P = 0.0000$, $\alpha = 0.0127$

1- The total number of subsamples is <2400 because for some of the first samples the amount of organic matter was not estimated.
2- Subsamples with an estimated volume of organic matter >30%.

Table 5. Results of goodness of fit test[1] for the horizontal distribution of populations of land snails, associated with three habitat types in the Sheep River Wildlife Sanctuary, in southwestern Alberta. Snails were recovered from 600 soil cores[2], in 1980 and 1981.

Habitat type	Month	$\bar{X}$	s^2	P
Poplar	May	4.68	590.25	0.0000
	June	2.24	19.52	0.0000
	July	2.86	20.44	0.0455
	August	2.74	29.59	0.0000
Mixedwood	May	0.72	3.84	0.3179
	June	0.56	2.55	0.0074
	July	1.06	119.92	0.0000
	August	0.48	4.12	0.0012
Spruce	May	3.90	245.37	0.0000
	June	6.84	440.71	0.0000
	July	7.96	413.69	0.0000
	August	3.12	67.79	0.0000

1- Based on comparisons against the Poisson distribution: α=0.0011
2- Diameter = 6.2 cm, volume = ca 600 cc.
X = average number of snails / sample.

Discussion

The distribution of soil dwelling gastropods is affected by a number of biotic and abiotic factors (Boycott 1934), temperature and humidity being very important (Likhachev and Rammel'meier 1952). Soil pH is not important (Karlin 1961; Hyman 1967), but the nature of the overstorey vegetation is strongly correlated with the presence of several species of pulmonate gastropods (Burch 1956; Karlin 1961; Lowell 1974; Boag and Wishart 1982). Presence of lime (Boycott 1934, Likhachev and Rammel'meier 1952) and/or other minerals may also affect snail distribution (Burch 1955, Karlin 1961). Because of the complexity of the environment, Karlin (1961) and Bishop (1977) expressed the necessity of a detailed description of all factors which may have an effect on the gastropods' populations (*e.g.*, physiographic features, pedochemical characteristics, climate and vegetation).

Sampling techniques are also a critical factor, particularly for quantitative studies of gastropod populations. In fact, Bishop (1977) and Boag (1982) stressed the necessity of a careful choice of the sampling procedure to minimize the possibilities of biased results.

Incomplete descriptions of the experimental conditions may cause difficulties in comparing different experiments. For example, in this study I recovered the highest proportion of snails from a coniferous forest (Table 1). This is consistent with the results of Clarke *et. al.* (1968), Gleich and Gilbert (1976), Kearney and Gilbert (1978) and Walden (1981). On the other hand, Karlin (1961) and Boag and Wishart (1982) found very few gastropods in coniferous forests, and Hyman (1967) considers the latter a poor habitat for terrestrial molluscs. I believe that the discrepancy between these results depends on differences in the amount of litter, and possibly moisture, in the respective sampling areas. Unfortunately, Karlin (1961) and Boag and Wishart (1982) give no information on litter, and Karlin (1961) does not even provide a description of the sampling technique used. The role of the litter as a factor in snail abundance has received little attention, although its presence is correlated with the presence of snails (Burch 1955, Cameron 1973). Likhachev and Rammel'meier (1952) maintain that molluscs do not use conifer litter as food. This may be true, but the results of this study suggest that snails are closely associated with decaying wood and leaves, regardless of the forest type (Table 4). If

snails do not use conifer litter directly, they must use nutrients derived from it, by feeding, for example, on fungal mycelia. For example, *Discus rotundatus* feeds on mycelia and algae (Chatfield 1975) which abound in the litter of the Spruce forest, where I took my samples. The fact that a significant proportion of fresh snail shells was found deeper than 5 cm suggests that the results, based on those techniques that sample only the superficial layers of the soil (for example, Coney *et al*. 1982), should be carefully used. If these techniques rely on the assumption that the proportions of gastropods do not change over time, in the top layers of soil, then the reliability of those techniques should be questioned. In this study the total number of gastropods showed little variation (Table 1); however, their proportions at different depths in the soil changed greatly from May to August (see Section V).

The results from this study suggest that the gastropods were highly clumped. For this reason, taking samples at regular intervals (for example, Lankester and Anderson 1968) should be avoided, at least for studies of a quantitative character. Random choice of the sampling sites has been recommended (for example by Hairston *et al*. 1958, and Bishop 1977). In fact, if the snails are clumped, as in this study (Table 4), only random sampling will eliminate the chance of taking samples in locations systematically coinciding with areas of either very low or very high snail density. Since sampling techniques that estimate population size of terrestrial gastropods 'should be placed on a firm quantitative base' (Bishop 1977:61), random sampling may often be required for a valid statistical analysis (Kirk 1968). If the sampling sites are regularly distributed along a transect (for example, Boag and Wishart 1982), relocating the plots at distances chosen at random would increase the reliability of that technique.

V. THE RELATIONSHIP BETWEEN TIME, VEGETATION AND CLIMATE, AND THE VERTICAL DISTRIBUTION OF TERRESTRIAL SNAILS IN THREE HABITAT TYPES IN SOUTHWESTERN ALBERTA.

Introduction

The distribution of pulmonate gastropods in the soil is affected by several factors, food and shelter being important (Boycott 1934, Likhachev and Rammel'meier 1952). The amount of organic litter seems to be correlated with the presence of molluscs in the soil (Burch 1955, this study: Section IV) and their numbers decrease proportionally with the depth (see Section IV). The three habitat types analyzed in this study (Poplar stand, Mixedwood, and Spruce forest) differ considerably in the composition and abundance of understorey and of overstorey vegetation, as well as in moisture content in the soil, and in the quantity and the quality of organic litter (see Study Area). Since the leaves of trees are the main contributors to the formation of organic litter (Lutz and Chandeler 1946), it was expected that tree composition would be a very important factor in the distribution of litter-dwelling gastropods. This should be especially true for detritivorous molluscs. On the other hand, the understorey vegetation could affect the distribution of herbivorous gastropods. Results from a preliminary study, in which random samples of litter were taken and hand searched for molluscs (Section IV), suggested a lack of correlation between ground vegetation and snail abundance. Similarily, Getz (1974) and Boag and Wishart (1982) found no correlation between herbaceous and shrubby vegetation and large and small species of snails respectively. Their suggestion is based on descriptive analyses, and, in this study, the expected lack of that correlation was quantitatively tested. In addition, the vertical distribution of terrestrial gastropods in the three habitat types chosen (see Study Area) was investigated over time to determine whether it changed during the frost-free season. The contribution of temperature and precipitation to these changes, was also investigated.

Methods and Materials

Core samples (600) of soil were collected monthly from May to August in three habitat types in the Bow Crow Forest of southwestern Alberta (see Study Area), and the shells of the terrestrial gastropods present in the samples were recovered (see General Methods). Temperature was recorded with a thermograph (Peabody Ryan, mod.'J') flush with the soil surface in the Poplar forest, from September 1980 to January 1981, from March 1981 to August 1981, and from October 1981 to December 1981. Temperature data for the month of June were lost because of a malfunction of the instrument. Precipitation was also recorded from June 1980 to August 1980, and from May 1981 to August 1981, with a plastic garden pluviometer installed at the R. B. Miller Biological Station of the University of Alberta, located within the study area.

The coverage of the understorey vegetation was measured using a quadrat-sampling technique (see General Methods). A multiple correlation analysis (Zar 1974) between the number of snails of different species recovered, and the coverage values of the herbs and shrubs found at the sampling sites, was accomplished using a BMDP computer programme (Dixon and Brown 1979).

Results

The 1858 individual shells recovered from the 600 core-samples, taken in the three habitat types, were distributed among nine species (Table 5). Specimens of five more species (*Lymnaea bulimoides, Physa gyrina, Planorbis* sp., *Vitrina alaskana,* and *Vallonia* sp.) were recovered from the samples, but these were not included in the analyses because they were extremely rare and/or their shells were of questionable freshness. The relative contribution of each species varied considerably among the three types of forests. Members of the Pupillidae were the most abundant snails in all three habitat types, representing respectively ca. 66% of the total number of fresh shells recovered from the Poplar forest, ca. 70% of those from the Mixedwood, and ca. 89% of those from the Spruce forest (Table 5). Any Pupillidae, with shells <1.2 mm high were placed into one common group (Pupillidae: immatures), because of the difficulty of identificaton to the species level. The four species of Pupillidae recovered were present in varying proportions in the three habitat types. In the Poplar stand, for example, *Vertigo*

gouldi was the most abundant (45.8%); whereas, in the Spruce forest it was relatively scarce (3.4%, Table 6). By contrast, *V. modesta* was relatively poorly represented in the Poplar stand (4.0%), yet abounded in the Spruce forest (52.3%), being the dominant species (Table 6). *Discus cronkhitei* and *Euconulus fulvus* were common and well represented in all the three habitat types; whereas, *Punctum pygmaeum* and *Zonitoides arboreus* were present in the Poplar and in the Spruce forests, and very rare, or absent, in the Mixedwood (Table 6).

The average size of the shells showed little variation during the period of the study (table 7).

The proportion of snails found in the upper layers of the soil increased from May to August (Figures 3, 4 and 5). In the Mixedwood, where the litter is very thin, this trend is much less clear.

The results suggest a positive correlation between *Equisetum arvense* and some species of gastropods (Table 8). Correlation coefficients for lichens, *Rubus* spp. and *Fragaria virginiana* were also significant (Table 8). Nevertheless, the highest value obtained for r^2, the coefficient of coordination (Zar 1974), was 0.174, suggesting very weak and inconclusive correlations. For this reason, in this study, all the correlations recorded were interpreted as non significant.

Discussion

Snail diversity is positively correlated with tree diversity (Getz 1974), and factors like calcium and magnesium content (Boycott 1934, Burch 1955). On the other hand, the scarcity of terrestrial gastropods in some areas has been attributed to the nature of the tree cover. Karlin (1961), for example, found very few snails in samples from coniferous forests. Similarily, Boag and Wishart (1982) recorded the greatest numbers of gastropods in deciduous forests. In their study the snail density was correlated with the stem density of the nearby trees. On the contrary, in this study, the Spruce forest proved to be the richest, in both number of snails and species diversity (Section V). Based on the very high correlation that I found, I suggest that abundance of litter is a critical factor for the presence of molluscs (Section IV). Nevertheless, it would be reasonable to expect different gastropod species to be affected to different degrees by the composition of

Table 6. Number and percent of fresh shells of terrestrial gastropods recovered from 600 core samples of soil, taken from three habitat types in the Sheep River Wildlife Sanctuary, in southwestern Alberta, during the period May-August, 1980 and 1981.

		Poplar		Mixedwood		Spruce	
Pupillidae	*Columella* spp.[1]	24	3.8%	2	1.4%	152	13.9%
	Vertigo gouldi	287	45.8%	35	24.8%	37	3.4%
	Vertigo modesta	25	4.0%	37	26.2%	570	52.3%
	Immature[2]	77	12.3%	24	17.0%	210	19.3%
Endodontidae	*Punctum pygmaeum*	43	6.9%	2	1.4%	20	1.8%
	Discus cronkhitei	85	13.6%	24	17.0%	44	4.0%
Zonitidae	*Euconulus fulvus*	68	10.9%	15	10.6%	30	2.8%
	Retinella electrina	3	0.5%	2	1.4%	15	1.4%
	Zonitoides arboreus	14	2.2%	-	0%	13	1.2%
Total		626		141		1091	

1- *C. alticola* and *C. edentula* equally represented.
2- *Columella* spp., *Vertigo gouldi*, *V. modesta*.

Table 7. Average size of terrestrial molluscs recovered from 600 soil cores, from three habitat types in the Sheep River Wildlife Sanctuary, in southwestern Alberta, from May to August, 1980 and 1981.

Species	May		June		July		August	
				Poplar				
	n	$\bar{X}$	n	$\bar{X}$	n	$\bar{X}$	n	$\bar{X}$
Columella spp.[1]	23	2.4	0	-	1	2.2	0	-
Vertigo gouldi	71	1.8	58	1.8	73	1.8	85	1.8
Vertigo modesta	5	2.1	4	2.1	6	2.0	10	2.0
Pupillidae (imm.)	16	1.1	15	1.0	20	1.0	26	1.1
Punctum pygmaeum	26	1.1	4	1.2	8	1.3	5	1.2
Discus cronkhitei	57	2.4	12	1.8	12	3.2	4	3.4
Euconulus fulvus	29	1.8	14	1.6	19	1.2	6	1.7
Retinella electrina	0	-	3	1.0	0	-	0	-
Zonitoides arboreus	7	1.8	2	1.9	4	2.2	1	1.9
				Mixedwood				
Columella spp.[1]	1	2.8	1	3.4	0	-	0	-
Vertigo gouldi	11	1.5	8	1.9	7	1.8	9	1.8
Vertigo modesta	9	2.0	7	2.1	20	1.9	1	2.2
Pupillidae (imm.)	5	1.1	4	1.1	11	1.1	4	1.1
Punctum pygmaeum	0	-	1	1.4	1	1.1	0	0
Discus cronkhitei	4	2.8	3	2.9	10	2.3	7	.8
Euconulus fulvus	5	1.5	4	1.9	3	1.8	3	1.9
Retinella electrina	1	1.1	0	-	1	1.0	0	-
				Spruce				
Columella spp.[1]	40	2.3	44	2.4	44	2.3	24	2.2
Vertigo gouldi	4	1.9	7	1.9	16	1.8	10	1.8
Vertigo modesta	78	2.1	185	2.0	229	2.0	78	1.9
Pupillidae (imm.)	52	1.1	54	1.1	11	1.1	4	1.1
Punctum pygmaeum	3	1.2	11	1.2	4	1.3	2	.3
Discus cronkhitei	6	1.8	14	2.5	10	2.3	7	2.1
Euconulus fulvus	6	1.8	13	1.7	6	1.5	5	1.7
Retinella electrina	4	2.3	6	1.3	1	4.4	4	2.1
Zonitoides arboreus	2	2.3	8	1.2	2	3.4	1	1.4

[1]- *C. alticola* and *C. edentula* equally represented.

Table 8. Values of *r* for multiple correlation between numbers of snails and vegetation cover on three Habitat types in the Sheep River Wildlife Sanctuary in southwestern Alberta. Only the significant values are shown.

	Lichens	*Equisetum arvense*	*Rubus* spp.	*Fragaria virginiana*	*Lathyrus ochroleucus*
Columella spp.[1]	0.1269	0.4170	0.1801	-0.1163	-0.1254
Vertigo gouldi	0.1619				0.1551
Vertigo modesta	0.1419	0.3227	0.1583	-0.1090	-0.1331
Discus cronkhitei		0.1130			
Punctum pygmaeum		0.1170			
Euconulus fulvus		0.1043			

1- *C. alticola* and *C. edentula* equally represented.

Figure 3. Vertical distribution of terrestrial snails in the Poplar Stand, in the Sheep River Wildlife Sanctuary in southwestern Alberta, from May to August 1980 and 1981, recovered from 200 core samples.

POPLAR

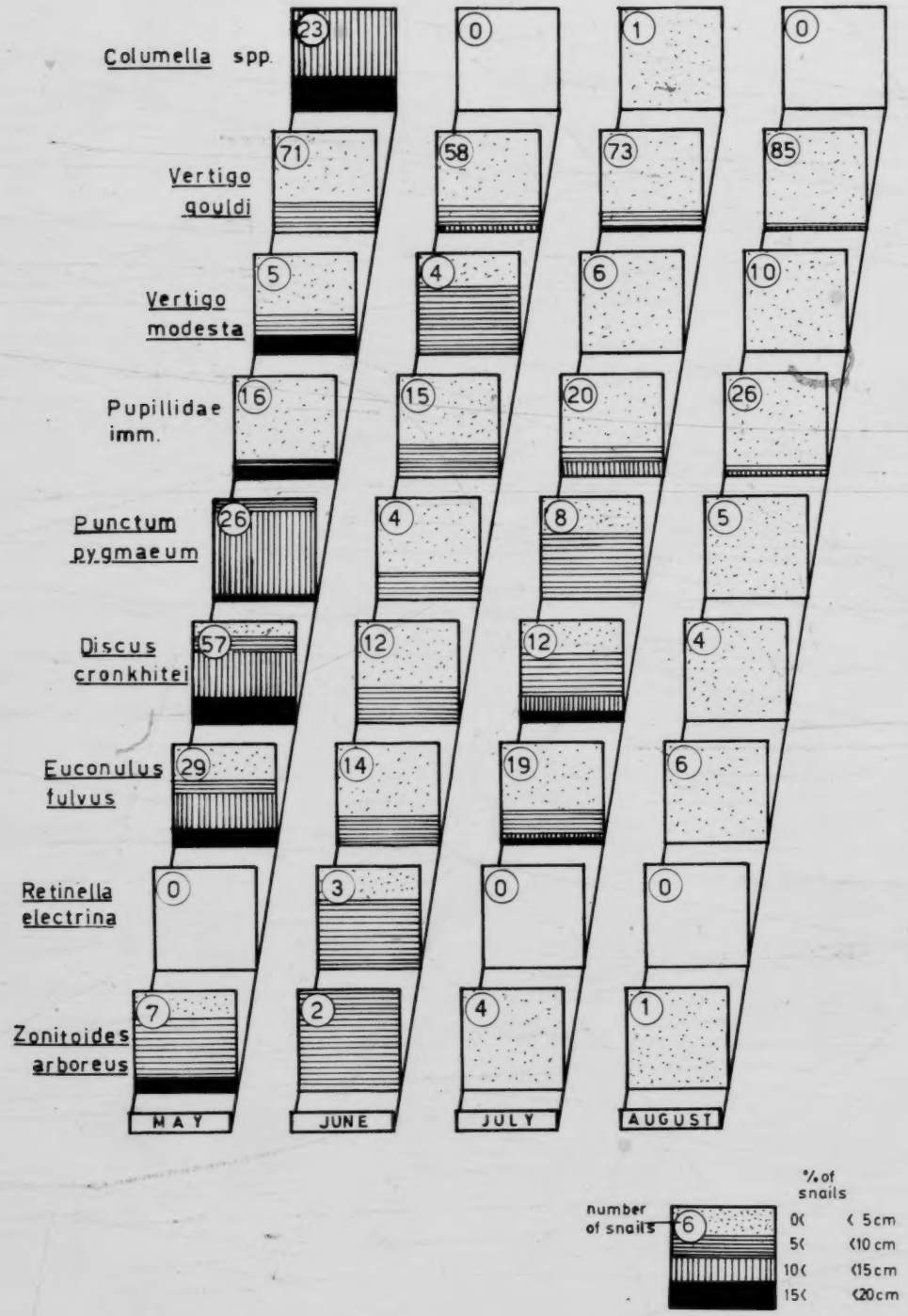

Columella spp.
23
0
1
0
Vertigo gouldi
71
58
73
85
Vertigo modesta
5
4
6
10
Pupillidae imm.
16
15
20
26
Punctum pygmaeum
26
4
8
5
Discus cronkhitei
57
12
12
4
Euconulus fulvus
29
14
19
6
Retinella electrina
0
3
0
0
Zonitoides arboreus
7
2
4
1
MAY
JUNE
JULY
AUGUST
% of snails
number of snails
6
0(< 5cm
5(<10 cm
10(<15cm
15(<20cm

Figure 4. Vertical distribution of terrestrial snails in the Mixedwood, in the Sheep River Wildlife Sanctuary, in southwestern Alberta, from May to August 1980 and 1981, recovered from 200 core samples.

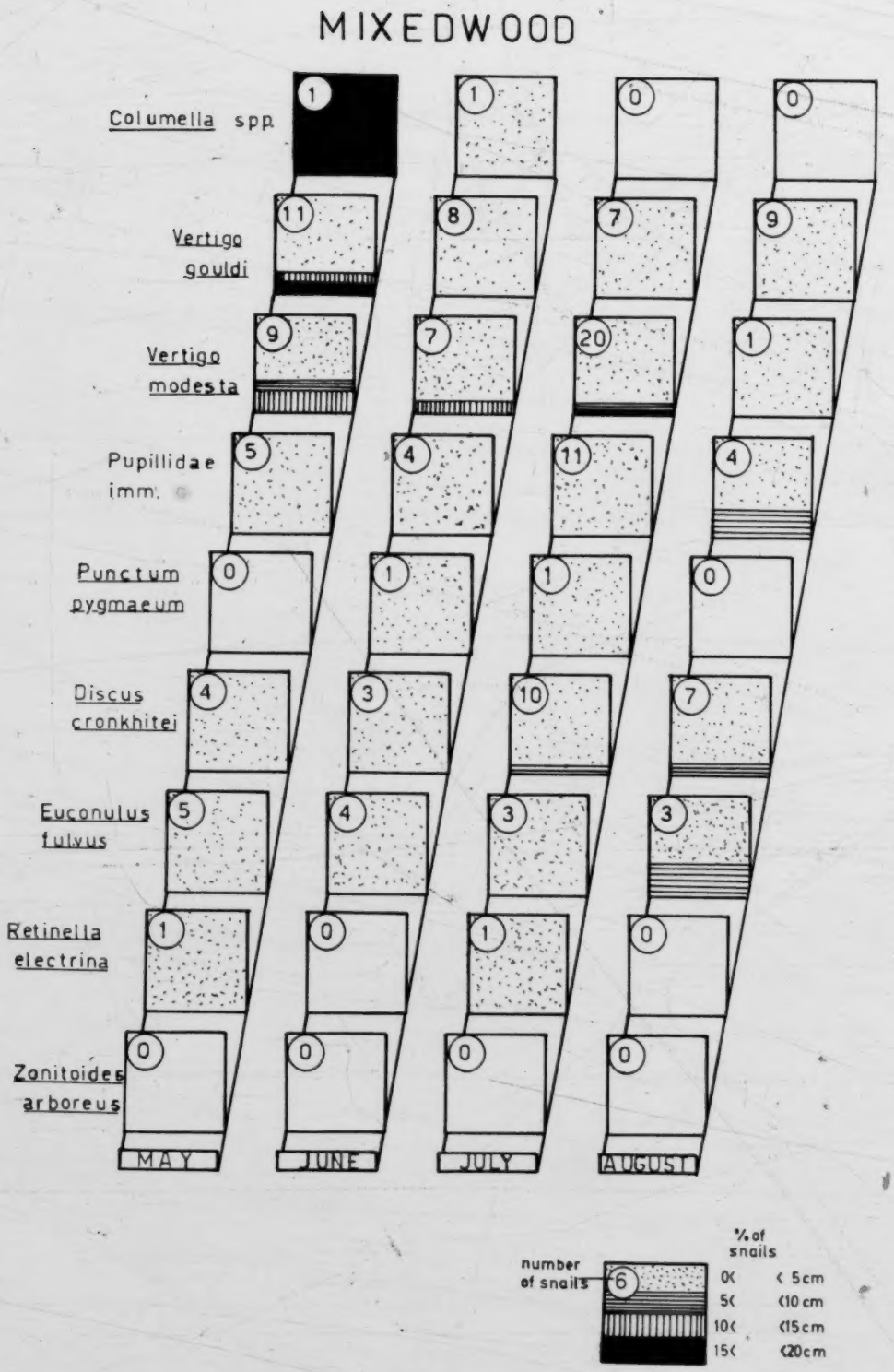
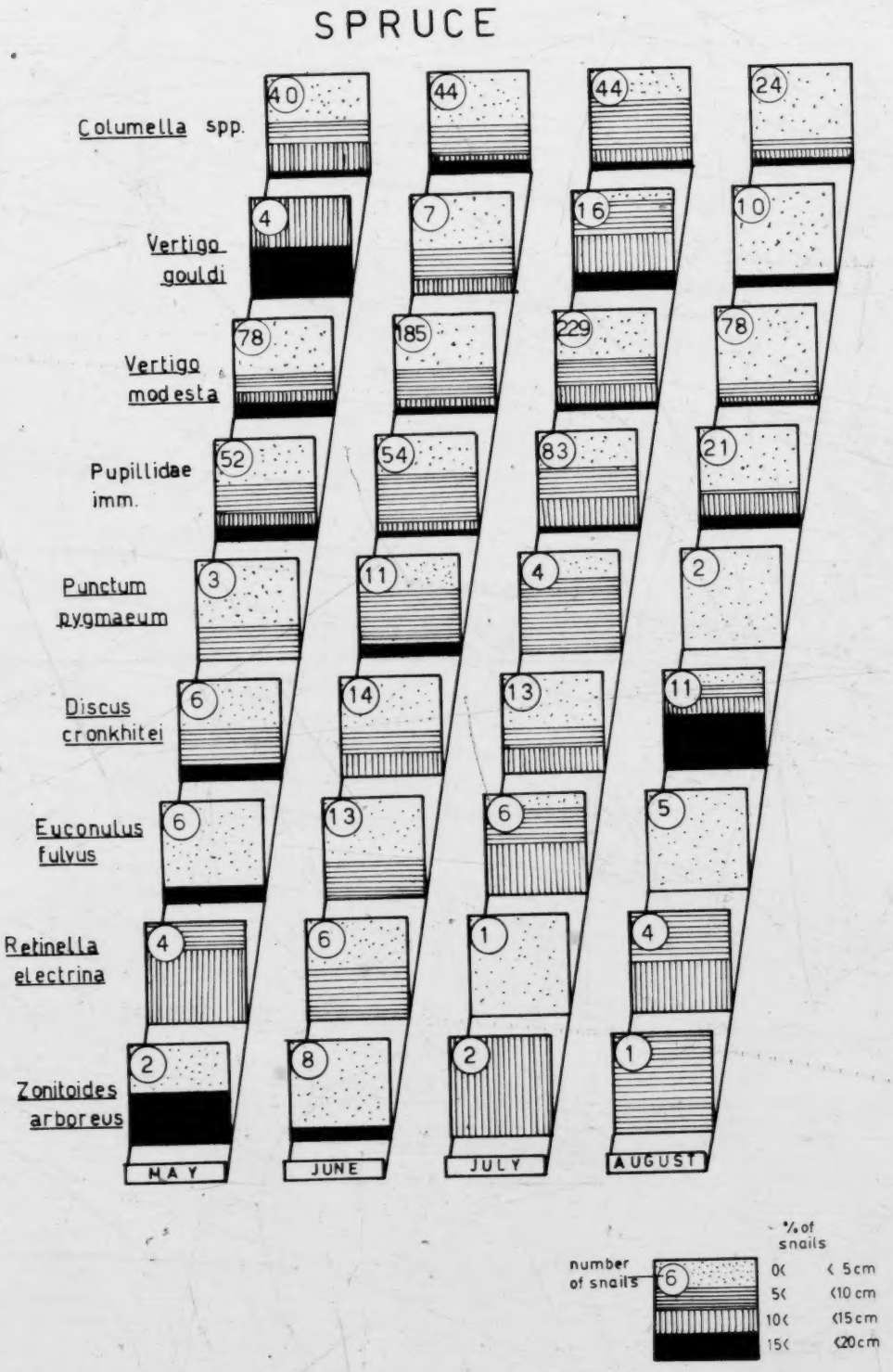

MIXEDWOOD
Columella spp.
Vertigo gouldi
Vertigo modesta
Pupillidae imm.
Punctum pygmaeum
Discus cronkhitei
Euconulus fulvus
Retinella electrina
Zonitoides arboreus
1 1 0 0
11 8 7 9
9 7 20 1
5 4 11 4
0 1 1 0
4 3 10 7
5 4 3 3
1 0 1 0
0 0 0 0
MAY
JUNE
JULY
AUGUST
number of snails
6
% of snails
0(< 5cm
5(<10 cm
10(<15 cm
15(<20cm

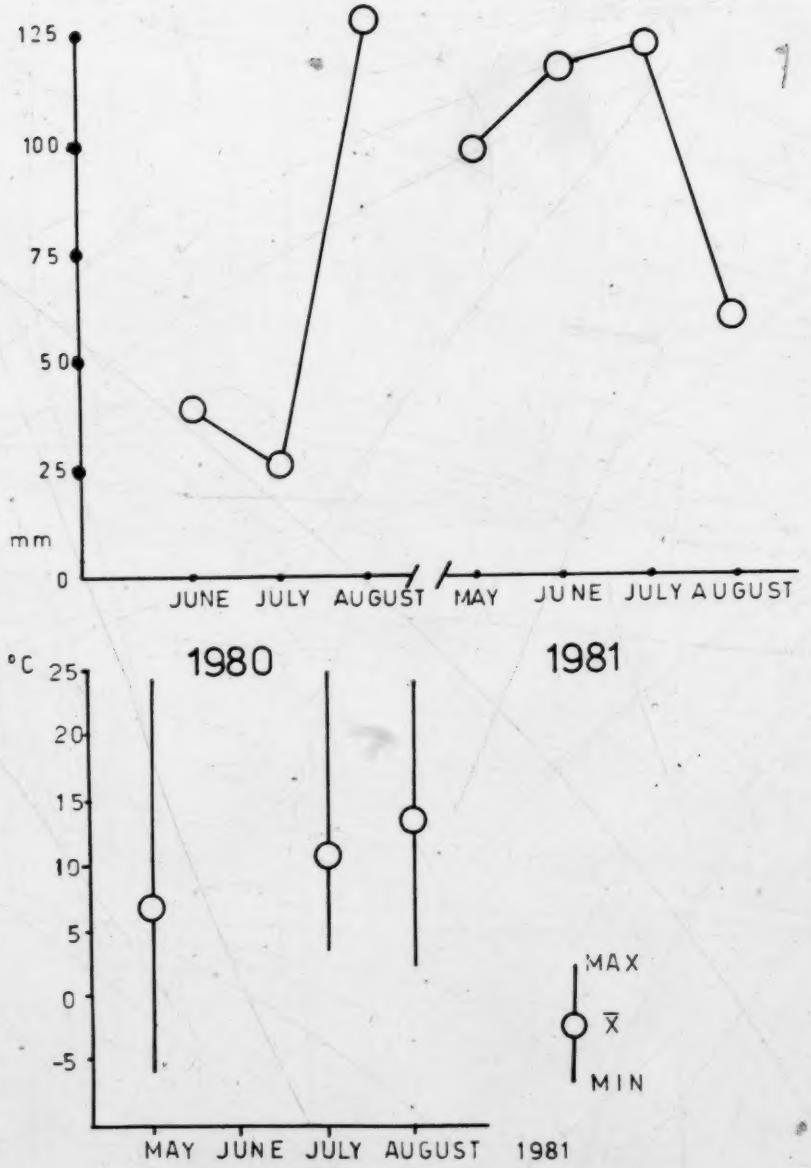
Figure 5. Vertical distribution of terrestrial snails in the Spruce Forest, in the Sheep River Wildlife Sanctuary, in southwestern Alberta, from May to August 1980 and 1981, recovered from 200 core samples.


SPRUCE
Columella spp.
Vertigo gouldi
Vertigo modesta
Pupillidae imm.
Punctum pygmaeum
Discus cronkhitei
Euconulus fulvus
Retinella electrina
Zonitoides arboreus
40
44
44
24
4
7
16
10
78
185
229
78
52
54
83
21
3
11
4
2
6
14
13
11
6
13
6
5
4
6
1
4
2
8
2
1
MAY
JUNE
JULY
AUGUST
number of snails
6
% of snails
0(< 5cm
5(<10 cm
10(<15 cm
15(<20cm

the litter. This is, reportedly, dependent on their ecological tolerances (Walden 1981). The two species of *Vertigo*, *V. gouldi* and *V. modesta*, collected in this study were present in varying proportions in the three habitat types sampled, and tended to occupy forests with litter of different composition. In particular, *V. modesta* was more common in Spruce forest litter, whereas *V. gouldi* was more abundant in Poplar stand (see Table 5). There was little overlap between *Vertigo gouldi* and *V. modesta* in pure or nearly pure stands (Table 5), but the overlap increased proportionally with the increasing mixing of different types of litter. This last situation was, in fact, found in the Mixedwood forest, where coniferous and deciduous trees contributed approximately equally to the formation of the litter (see Study Area). In the samples from this habitat type, both species of *Vertigo* were recorded in nearly equal proportions (Table 5). Moreover, the much higher proportion of the detritivorous *Columella* spp., 'oligotrophy-tolerant' (Walden 1981), in the Spruce forest, compared to the Poplar forest (Table 5), further supports the suggestion that litter composition affects snail communities. This selectivity was not apparent in the members of the other two families of pulmonate gastropods (Endodontidae and Zonitidae) recorded in this study. Species with broad tolerance limits are found in a variety of habitat types (Boycott 1934, Burch 1956, Silvola 1964), and the fact that Boag and Wishart (1982) found this to be true for *Euconulus fulvus* and *Discus cronkhitei*, similar to the results from this study, suggests that these species are more tolerant than others.

Uminski and Focht (1979) recorded a very low density of terrestrial gastropods in July and August, and they suggest that the snails dig into the ground to avoid summer drought. In this study, abundant precipitation was recorded during the sampling period (see Figure 6), and the maxima and minima recorded vary considerably between 1980 and 1981. But this does not seem to have affected the numbers of the snails, and no significant difference was found between the numbers of gastropods collected in the two years (see Section III). Boag and Wishart (1982) recorded maximum numbers of pulmonate gastropods in August, from 1979 to 1981. This is what might be expected, since data from this study suggest that in August the majority of terrestrial gastropods inhabit the top 5 cm of the litter (Figures 3, 4 and 5). Boag and Wishart (1982) employed a sampling technique based on attracting the gastropods under a series of masonite

Figure 6. Total precipitation recorded in 1980 and 1981 at the R. B. Miller Biological Station, within the study area, and mean temperatures recorded in the Poplar stand in 1981.


125
100
75
50
25
mm
0
JUNE JULY AUGUST
MAY JUNE JULY AUGUST
1980
1981
°C 25
20
15
10
5
0
-5
MAX
X̄
MIN
MAY JUNE JULY AUGUST 1981

squares. But they may well have underestimated numbers in the months May, June and July. In fact, in this study, almost all the species of gastropods recorded were more abundant in the upper layers of the litter (0-5 cm) in August (Figures 3, 4 and 5). This seems to be particularly true of the family Pupillidae. This fact may be related to average temperature, which in 1981, and likely in 1980 as well, increased constantly, from May to August (Figure 6). Temperature and high humidity affect vertical distribution of terrestrial gastropods (Cameron 1970, this study: Justification), Precipitation was abundant in 1980 and 1981 in the area where this study was undertaken (Figure 6). This fact, together with the rising temperatures from May to August, may explain the high number of snails found in the top layers of the soil.

The average individual size of the shells showed little variation during the period of the study (Table 7). Nevertheless, in the Spruce forest, I recorded a decrease in size for all adult Pupullidae. This suggests a similarity in the life cycle of the Pupillidae, but the correlation between age and size in the gastropods is very controversial (Comfort 1957). For this reason, data on snail size should be used with caution when interpreting mollusc life cycles.

As expected, there was no correlation, overall, between the understorey vegetation and the presence of snails ($r^2<0.04$) in the habitat types sampled. In one case, however, (*Equisetum arvense*), a higher correlation was found ($r^2=0.17$, which is still a very low value for r^2). This could be due to the fact that *E. arvense* is associated with moist habitats (Moss 1974); thus, the correlation observed is more likely to have existed between the snails and the moist litter.

VI. CONCLUDING DISCUSSION

Soil sifting techniques , although very time consuming, are much more exhaustive and less biased than others (Walden 1981). The main problems associated with them are that fragile shells are broken, and smaller shells are underestimated, when the residue is hand searched (Boag 1982). I believe that, using a wet-sifting technique and a dissecting microscope, I eliminated or, at least, greatly reduced, these two problems in this study. On the other hand, slugs cannot be recovered with this technique, and very fragile shells may still be broken by the process. For this reason, I did not include in this study the slug *Deroceras laeve* and the snail *Vitrina alaskana*, present in my study area (Boag and Wishart 1982).

Boag and Wishart (1982) suggested that the snails, in the litter, are horizontally clumped, and that their distribution is not correlated with understorey vegetation. This was based, by implication, on descriptive data. In this study, I provide evidence of a quantitative character, that supports their suggestions.

Some small litter-dwelling molluscs exist as relatively stable populations (Bishop 1977). I found that the total number of snails in the soil underwent little changes, from May to August, 1980 and 1981. However, the gastropods showed a marked change in their vertical distribution, in the same period. This fact may lead to underestimating mollusc populations, from time to time, when only the surface layer of the soil is sampled (for example, Uminski 1979, Platt 1981). Boag and Wishart (1982) recorded a decline, after August, in the numbers of *Euconulus fulvus* and *Vertigo* spp. But that decline could be explained by a migration of the gastropods into deeper locations in the soil, from whence they had come earlier in the season. In fact, from this study, August is the month when all gastropods species seem to have moved in the top 5 cm of soil. For this reason August is, potentially, a critical time for the completion of the life cycle of some bighorn sheep lungworms (*Protostrongylus* spp.), which, reportedly, are capable of using as intermediate hosts, some of the gastropods species recorded in this study (Forrester 1971, Latson 1977).

I provided data on gastropod shell density (Table 5). It is possible that I overestimated these numbers by including the shells of some freshly dead snails. But I believe that this overestimate, if it occurred, did not exceed 10%. Nevertheless, the

efficiency of the sifting technique that I used, should be assessed (Newell 1971, Kralka 1983), before using those data for estimating population densities.

Conflicting opinions are found in the literature regarding the effect of tree composition on the distribution of terrestrial gastropods. For example Baker (1942), Karlin (1961), Likhachev and Rammel'meier (1962) and Hyman (1967) suggest that coniferous forests are poor habitats for terrestrial snails. On the other hand, Gleich and Gilbert (1978) collected large numbers of gastropods form coniferous forests, and Walden (1981) found similar numbers of snails in deciduous and in conifer-dominated mixed forests. According to Kearney and Gilbert (1978) coniferous stands are as productive of gastropods as other forest types, and they describe a well-drained pine forest as one of the most productive habitat types. The Spruce forest is the habitat type were I recovered the higest numbers of snails. I attribute this to the fact that that forest had the most abundant litter of the three habitat types I studied. In fact, I found that snails were much more abundant in subsamples rich in organic matter, regardless of the habitat type. On the other hand, the different species differed in their proportions. Ground vegetation is not a critical factor for snail distribution (Getz 1974, Boag and Wishart 1982, this study), and temperature and precipitation were, probably, reasonably uniform in the area which included the three habitat types. For these reasons, I believe that the different proportions of gastropod species found, were due to litter composition, and, possibly, to different moisture content. Because of this, I suggest that, for terrestrial gastropod studies, information on quantity and, possibly, quality of the litter should be reported in the description of the study area.

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Appendix I. Coverage values (X of plant taxa recorded from three habitat types in the Sheep River Wildlife Sanctuary, in southwestern Alberta, from May to August, 1980 and 1981.

	Poplar				Mixedwood				Spruce			
Taxon	May	June	July	August	May	June	July	August	May	June	July	August
Lichens					3.7	5.8	0.7	2.5	3.5	5.2	3.7	3.0
Bryophytes	0.2	0.8		0.3	8.5	9.0	2.3	4.3	46.8	52.8	41.3	38.2
Equisetum arvense	2.5	0.2		0.7	0.3	0.8	0.7	0.8	16.3	22.3	26.8	26.8
Gramineae	45.2	55.8	69.0	59.8	21.8	22.3	24.0	24.2	10.5	15.7	8.3	14.7
Allium spp.		0.2				0.3		0.3			0.2	
Smilacina stellata	8.0	6.0	4.5	4.7	1.2	1.2	0.7	0.5	0.8	1.0	0.5	1.0
Anemone patens					1.3	2.2	0.2	1.3				
Mitella pentandra					0.3	0.7		0.8	4.7	11.8	8.7	5.2
Thalictrum venulosum	6.8	6.2	9.0	5.0	1.5	4.2	3.3	1.0			0.2	
Fragaria virginiana	4.7	7.3	6.2	5.3	15.0	15.3	15.3	14.8	7.8	5.0	5.2	7.2
Rosa woodsii	5.8	6.3	5.0	5.6	8.2	8.5	9.2	12.7	2.0	2.2	5.3	2.0
Rubus spp.	0.2	0.2	0.3	0.8	0.5	0.8	0.8	3.0	3.2	5.0	3.0	2.7
Hedisarum spp.						2.0	0.2	1.3				
Lathyrus ochroleucus	9.3	15.0	16.3	13.7	2.5	5.3	4.7	3.8	1.7	1.8	0.3	3.3
Vicia sp.	2.3	7.0	9.0	6.2	1.7	3.3	2.0	0.2		0.2		0.3

Geranium spp.	8.0	0.3	12.0	8.7	2.2	4.3	3.9	2.0	3.0	1.5	2.2	0.5
Viola palustris	1.7	1.2		1.0	0.8					0.2		
Sheperdia canadensis					5.8	3.0	14.2	11.0	0.3	0.3		0.8
Epilobium angustif.	8.2	17.0	18.2	13.5	0.8	2.0	4.0	0.2	2.7	2.3	4.0	5.0
Heracleum lanatum	3.4	7.8	4.7	3.5	0.2		0.8			0.2		
Cornus canadense					0.8	0.7	3.2	2.0	1.9	4.5	5.3	3.7
Pyrolaceae					2.5	0.5	0.7	3.0	1.2		2.3	5.5
Arctostaph. uva-ursi	0.8				0.3	2.3	1.5	5.7				
Mertensia paniculata					6.0	4.8	6.0	6.5	8.0	4.3	2.8	3.7
Galium boreale	6.0	7.2	6.2	8.3	1.7	2.5	1.3	3.3	1.0	1.5	0.3	1.83
Linnaea borealis					2.3	7.0	7.2	4.0	5.2	2.5	0.2	8.7
Symphoricarpos vacc.	1.2	1.2		4.3	0.3	2.2	0.2	1.3				
Achillea millefolia	2.0	4.0	3.7	3.0	1.3	3.8	1.8	2.7	0.3			0.2
Arnica cordifolia					2.8	0.3	0.3		0.2		0.2	
Artemisia frigida	0.3	2.7	0.5				0.2					
Aster spp.	13.7	14.8	15.3	15.8	0.7	6.3	5.7	5.8			3.5	6.8
Erigeron spp.		1.3	0.3	1.2	4.0	5.7	1.7	6.2	0.2	1.0		
Petasites palmatus						0.2			1.0	3.7	2.7	5.0
Solidago canadensis	1.2	4.2	5.7	0.8			0.2					
Taraxacum officinale	0.2	1.0	0.7	0.3	4.2	8.8	3.4	5.0	2.3	1.3	1.0	1.8